

THE BIOLOGY AND FUNCTIONAL MORPHOLOGY OF
FOEGIA NOVAEZELANDIAE (BIVALVIA: ANOMALODESMATA:
CLAVAGELLOIDEA) FROM WESTERN AUSTRALIA

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ABSTRACT

As more representatives of the adventitious, tube-building anomalodesmatan Clavagelloidea are examined, a pattern of extraordinary adaptive radiation is being revealed. Despite its name, *Foegia novaezealandiae* is known only from the Holocene and Recent of Western Australia and is thus possibly very modern. A few tubes are held in the collections of the Western Australian Museum, Perth, and a single living individual has been collected from a hypoxic beach at Dampier, Western Australia. Like other clavagelloids, using a muscular pedal disc, *F. novaezealandiae* pumps interstitial water into its mantle cavity via the pedal gape, and hence the pedal slit and tubules of its anterior "watering pot" component of the adventitious tube.

Foegia novaezealandiae is similar to *Brechites vaginiferus* in being amyarian, except for minute anterior pedal retractor muscles in the latter. As with *B. vaginiferus* also, pallial retractor muscles effect siphonal and pedal disc retraction. The adventitious tube of *F. novaezealandiae* is more complex in that the shell valves are recessed and largely hidden externally by additional bulbous concretions of tube material secreted from anterior and posterior pallial crests. Also like *B. vaginiferus*, *F. novaezealandiae* pumps interstitial water into the mantle cavity, probably collecting interstitial bacteria and dissolved organic material as nutritional supplements. Unlike *B. vaginiferus*, however, *F. novaezealandiae* has an agglomeration of organic material and bacteria adhering to its highly convoluted periostracum anteriorly, particularly that of the pedal disc and thus inside the adventitious tube. Such bacteria may help detoxify the hydrogen sulphide contained in the interstitial water of the hypoxic sediment that *F. novaezealandiae* inhabits. However, *F. novaezealandiae* has a full complement of mantle cavity and intestinal organs for the processing of food filtered from the seawater above.

Key words: *Foegia novaezealandiae*, *Clavagelloidea*, adventitious tube formation, anatomy, tube function, watering-pot shell.

INTRODUCTION

The adventitious tubes of the diverse representatives of the Clavagelloidea d'Orbigny, 1843, constitute some of the weirdest and rarest bivalve structures. The most recent cladistic analysis of the Anomalodesmata by Harper et al. (2000) did not identify sister groups but noted that *Clavagella* and its allies first appeared in the Cretaceous, whereas *Brechites* and its allies are known from the Oligocene onwards. Savazzi (2000) also noted that representatives of the Clavagelloidea seem to fall into two groups comprising those that (i) have their left valve united into the fabric of an adventitious tube in the case of

endobenthic (*Stirpulina*) and epibenthic (*Dianadema*) genera, or a crypt in the case of nestling and boring species (*Clavagella*, *Bryopa*), with the right valve free inside it, and (ii) those in which both valves are incorporated into the structure of an adventitious tube, again in the case of endobenthic (*Brechites*, *Foegia*) and epibenthic (*Humphreyia*) genera.

The anatomies of species of *Clavagella*, *Bryopa* and *Dianadema* have been described by Soliman (1971), Savazzi (1999, 2000) and Morton (1984a, 2003), respectively, and those of representatives of *Brechites* and *Humphreyia* by Morton (1984b, 2002a, b). Two of the above genera, that is, *Dianadema* and *Humphreyia*, are known only from Australia,

and Smith (1971, 1976, 1998) and Lamprell & Healy (1998) catalogue the species recorded from that continent. These authors consider that in Australia the genus *Brechites* comprises three subgenera, that is, *Brechites*, s.s., plus *Penicillus* and *Foegia*, the second subgenus being represented by *B. (P.) philippinensis* (Chenu, 1843) and the third by *B. (F.) novaezelandiae* (Bruguière, 1789) and *B. (F.) veitchi* Smith, 1971. *Brechites (F.) novaezelandiae* is the type species of *Foegia* but, as noted by Smith (1971), other than for a description of its adventitious tube, virtually nothing else is known about it and there are no extant specimens with tissues available for study.

During January 2000, a research trip was made to Western Australia and a single living individual of *Foegia novaezelandiae* was collected. On this and subsequent visits, the small collection of tubes of this species in the Western Australian Museum was examined. Observations on the living animal and the collection of examined tubes are herein reported upon to provide an insight into the biology and anatomy of one of the strangest species, of one of the strangest superfamilies (Clavagelloidea) within the Bivalvia (Morton, 1981a, 1985a).

MATERIALS AND METHODS

The specimen of *Foegia novaezelandiae* was collected from intertidal mud on the beach adjacent to the leased property of Dampier Salt Co. Ltd., Karratha, Western Australia. It was buried anterior end down, that is, the watering pot, with the posterior tube projecting just above the mud surface.

As described for *Brechites vaginiferus* (Chenu, 1843) by Morton (2002a), the anterior end only of the adventitious tube of *Foegia novaezelandiae* was placed within a transparent tub with a lid that had a central hole in it to hold the tube in place and containing a suspension of Ehrlich's haematoxylin in seawater. The whole animal and tub was then placed in a much larger, also transparent, container of filtered seawater and left overnight. The living animal was subsequently dissected and the ciliary currents of the organs of the mantle cavity studied by application, again, of a seawater suspension of Ehrlich's haematoxylin. The specimen was fixed in 5% formalin eventually and, following routine histological pro-

cedures, sectioned transversely at 6 µm and every tenth section retained. Alternate slides were stained in either Ehrlich's haematoxylin and eosin or Masson's trichrome.

The nine specimens of *Foegia novaezelandiae* contained in the collections of the Western Australian Museum, Perth, were examined and the dimensions of all intact tubes measured to the nearest 1 mm. These were: greatest width, total length and length to the first growth (or possibly repair) increment.

ABBREVIATIONS USED IN FIGURES

AC	Anterior concretion
AN	Anus
APC	Anterior pallial crest
APCC	Anterior pallial crest cavity
AU	Auricle
CA	Ctenidial axis
CF	Cuticular fusion
CM	Circular muscle
CP	Ctenidial plica
C-P-V-CONN	Cerebro-pleural visceral connective
DD	Digestive diverticula
DK	Distal limb of the kidney
ES	Exhalant siphon
F	Foot
FPA	Fourth pallial aperture
H	Heart
HA	Haemocoel
HG	Hypobranchial gland
IBC	Infra-branchial chamber
ID	Inner demibranch
IE	Inner epithelium
ILP	Inner labial palp
IP	Inner layer of periostracum
IS	Inhalant siphon
K	Kidney
KC	Kidney concretion
KT	Kidney tubule
LM	Longitudinal muscle
LV	Left shell valve
MG	Mid gut
N	Nerve
O	Oesophagus
OA	Organic agglomeration
OD	Outer demibranch
OE	Outer epithelium
OLP	Outer labial palp
OP	Outer layer of periostracum
OS	Osphradium
OV	Ovary
P	Periostracum
PC	Posterior concretion

PD	Pedal disc
PE	Pericardium
PEG	Periostracal groove
PG	Pedal gape
PK	Proximal limb of the kidney
PL	Pallial line
PPC	Posterior pallial crest
PPCC	Posterior pallial crest cavity
PRM	Pallial retractor muscle
R	Rectum
RA	Renal aperture
RV	Right shell valve
S	Siphons
SA	Saddle
SBC	Supra-branchial chamber
SC	Sensory cell
SN	Siphonal nerve
SVI	Shell valve impression
TE	Testes
TMF	Transverse muscle fibres
V	Ventricle
VM	Visceral mass
VMG	Ventral marginal food groove

TAXONOMIC CONSIDERATIONS

Smith (1971) discussed the taxonomy of *Brechites* (*Foegia*) *novaezelandiae* (Bruguière, 1789). He regarded *Aspergillum agglutinans* Lamarck, 1818 (p. 430), and *A. novae-hollandiae* Chenu, 1843 (p. 3, pl. 4, fig. 8), to be synonyms. *Penicillus novae Zelandiae* Bruguière, 1789 (p. 129–130), was based on an ambiguous illustration in Favanne de Montcervelle & Favanne de Montcervelle (1780: 642, plate 79, fig. E), and misattributed to New Zealand. A neotype may be needed to stabilize the concept, because the original material has not come to light. No type material of *A. agglutinans* has been found. Two syntypes of *Aspergillum novaehollandiae* Chenu, 1843, are held in the collections of the Natural History Museum, London (1968668), and these are figured here (Fig. 1).

Gray (1858a: 313) differentiated *Foegia* Gray, 1847 (p. 188), from other genera in his Aspergillidae Gray, 1858, a junior synonym of the Clavagellidae Orbigny, 1844, in several important respects: "Umbo more or less covered with a swollen prominence in front; the whole of the valves except the umbo or nucleus enclosed in the tube; fringe indistinct, formed like the hole in the disk, of short thick separate tubes". The above description is generally correct, and because of other anatomi-

cal differences, I agree with Gray (1858a) that the genus *Foegia* is valid. It is possible that *Foegia* might date from Gray (1842: 77), where there is a definition but no named species. In any event, the type species of *Foegia* is *Penicillus novae Zelandiae* Bruguière, 1789, by monotypy in Gray (1847). The species under consideration is, therefore, *Foegia novaezelandiae* (Bruguière, 1789).



FIG. 1. *Foegia novaezelandiae*. The two syntypes of *Aspergillum novaehollandiae* (NHM London 1968668).

DISTRIBUTION

In the collection of the Department of Earth and Planetary Sciences of the Western Australian Museum are a number of local Holocene subfossils of *Foegia novaezelandiae*: 1. Kwinana (south of Perth). Dredged from Cockburn Sound, 3 specimens (WAM 69.1070a, b, c).

2. Fremantle. Dredged from a fishing anchorage, 1 specimen (WAM 70.2034).

In the collection of Recent Mollusca in the Western Australian Museum are 16 specimens of *Foegia novaezelandiae* collected from either Cockburn Sound, South Fremantle, Woodman's Point or Leighton Beach, all locations again just south of Perth. One was dredged from 1–2 fathoms (2–4 m), and all were dead when collected. Only nine tubes are intact.

Smith (1971) records that *Foegia novaezelandiae* occurs along "The central and south west coast of Western Australia and two specimens from the north coast of Queensland" (p. 152). Cotton (1961) does not record the species from South Australia, nor do Wells & Bryce (2000) from Western Australia, presumably because of its rarity. Smith (1976) illustrates (p. 201, map 3) the range of *F. novaezelandiae*. Lamprell & Healy (1998) agree with this distribution pattern and report that the species occurs from depths of 3–22 m in sand. The record herein, from Dampier, though intertidal, is within the distribution range described, and therefore *F. novaezelandiae* is a Southern Hemisphere, warm temperate-tropical species.

BIOLOGY

The single specimen from the Dampier Salt Co. Ltd. lease at Karratha, Western Australia, was collected from the intertidal of an unnamed muddy beach, the landward drainage onto which has been restricted by construction of a bund to create solar salt pond "0". The seaward remnant of the original creek which drained onto the beach, lies opposite and is divided into two outlets by West Intercourse Island. Mangroves fringe the beach: an *Avicennia* forest to the seaward is followed landward, in succession, by *Rhizophora* scrub, *Avicennia* scrub, and (locally) *Ceriops-Avicennia* heath grading into a salt flat. The main water influence here is the tides because the hypersaline (salinities > 40‰), drainage from the land, as reported upon by Morton

(2002a) for this part of Western Australia, has been halted by construction of the bund and causeway for pond "0". This has thus in turn adversely impacted not only beach dynamics but also interstitial water character. Whether

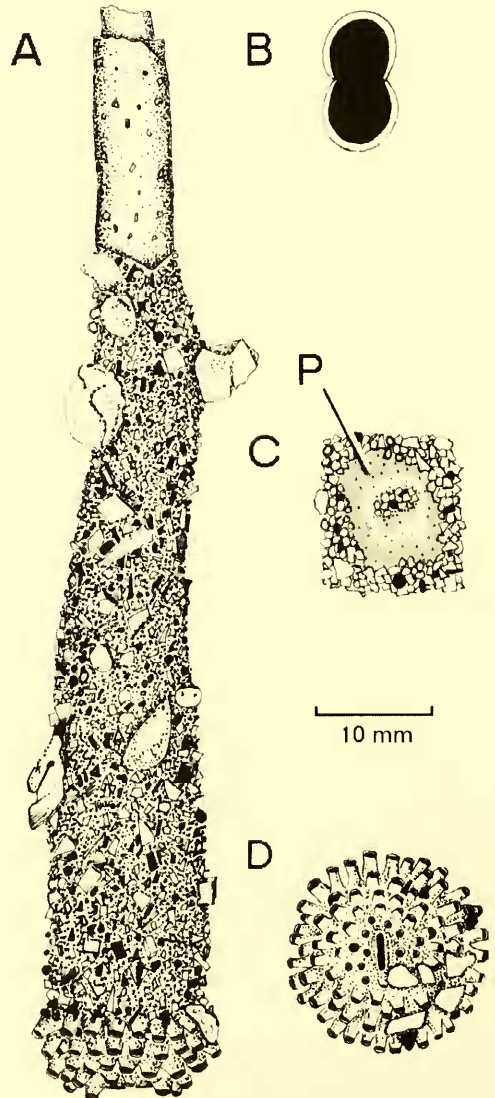


FIG. 2. *Foegia novaezelandiae*. A. The adventitious tube; B. the siphonal tube as seen from the posterior aspect; C. a closer view of the tube showing the calcareous tube and periostracum beneath the adhering detritus and D, the watering pot as seen from the anterior aspect. Note the dorso-ventrally aligned pedal slit (for abbreviations see pp. 38–39).

natural or perturbed, the substratum of sandy-mud in this *Foegia novaezelandiae* habitat is hypoxic, and the specimen was oriented vertically in it with the posterior end of the tube projecting above the sediment surface by some 10 mm. Semeniuk & Wurm (1987) describe in broad terms the characteristics of the shore seaward of pond "0" and provide basic maps (figs. 21, 22) of the area.

ANATOMY

Adventitious Tube

The nine tubes of *Foegia novaezelandiae* in the collections of the Western Australian Museum range in total length from 69–98 mm and in maximum width from 13–16 mm. The living individual from Dampier was 130 mm long and 15 mm wide. Some tubes in the collection have either a single growth increment or a repair at a length ranging from 80–94 mm. The Dampier individual has two (Fig. 2A). The relationships between tube width and total tube length and length to the first growth increment or repair are illustrated in Figure 3. Where there is no growth increment, the two measurements are

the same. Although the correlations are poor, the lines of best fit are similar. Four individuals, each with one growth or repair mark on the tube, lie on the right side of the plot suggesting that any such increment occurs at a length of between ~ 85–100 mm. The above implies that the adventitious tube is secreted but once when the contained animal becomes an adult, but that it can be subsequently extended or repaired posteriorly, as in *Brechites vaginiferus* (Morton, 2002a).

The tube of the living *Foegia novaezelandiae* is illustrated in Figure 2. The main shaft of the tube (Fig. 2A) is covered in sand grains and other hard detritus, except posteriorly and anteriorly at the watering pot disc. Posteriorly, there are two growth (or repair) increments, both secreted internal to the preceding one. These are covered sparsely in detritus and raised above the sediment surface. Viewed from the posterior aspect (Fig. 2B), the tube aperture is 8-shaped in cross-section matching the configuration of the siphons, which project up into it. In places, the shell debris is worn away from the tube beneath exposing the calcareous tube with a thin adhering film of periostracum (Fig. 2C). Seen from the anterior end (Fig. 2D), the watering pot disc has

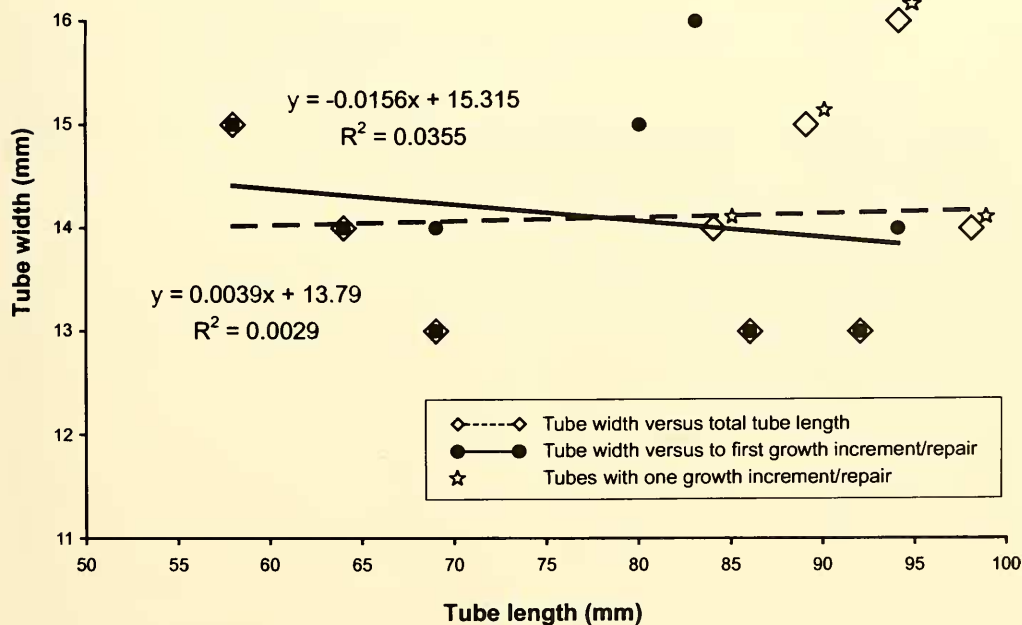


FIG. 3. *Foegia novaezelandiae*. The relationship between adventitious tube width and (i), total length and (ii), length to the first growth (or repair) increment.

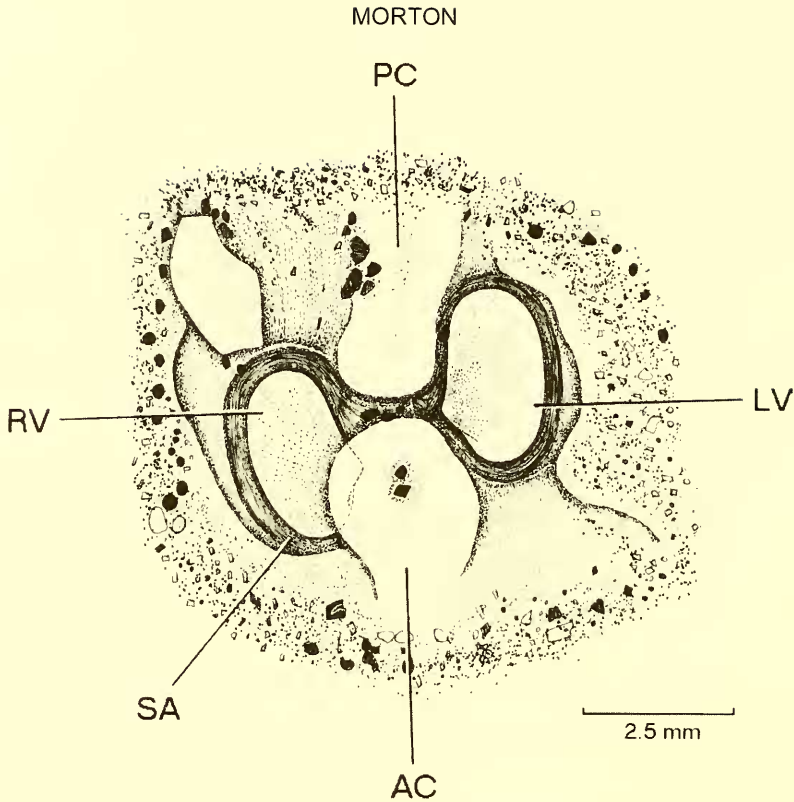


FIG. 4. *Foegia novaezelandiae*. A view of the dorsal surface of the adventitious tube showing the true shell valves and enclosing anterior and posterior bulbous projections (for abbreviations see pp. 38–39).

a dorso-ventrally aligned pedal slit and an array of open tubules which, as shown by Gray (1858a), do not have a distinct “fringe” separating it from the tube’s shaft, as is the case in *Brechites vaginiferus* and where it is identified as a distinct “line” (Morton, 2002a: fig. 1).

Tube Function

When the watering pot of the living individual of *Foegia novaezelandiae* was placed in a suspension of Ehrlich’s haematoxylin in seawater, the animal clarified it within 12 hours. Thus, as with *Brechites vaginiferus* (Morton, 2002a), *F. novaezelandiae* pumps interstitial water into the mantle cavity through the pedal slit and tubules that constitute the watering pot.

Shell

As noted by Gray (1858a), the shell of *Foegia novaezelandiae* is covered by two, anterior

and posterior, bulbous secretions and is generally hidden within the fabric of the adventitious tube. However in one specimen in the Western Australian Museum collection (from Cockburn Sound, (i) of (iv) specimens collected in 1965; broken base only; S 14232), the shell valves are partly visible. This specimen was cleaned carefully with dilute nitric acid, to remove sand grains and other debris and is illustrated in Figure 4. The two shell valves have parted and are ~ 3 mm long. They are equivalve and inequilateral, that is, anteriorly foreshortened and posteriorly elongate, and thus of the same general form as in all clavagelloids hitherto described, for example, *Brechites vaginiferus*, *Humphreyia strangei* and *Dianadema multangularis* (Morton, 2002a, b, 2003). The umbones are slightly pointed, and there is a trace of a radial sculpture of periostracal spinules, similar to those described for *Lyonsia hyalina* by Prezant (1979a) and for the clavagelloids listed above. Around

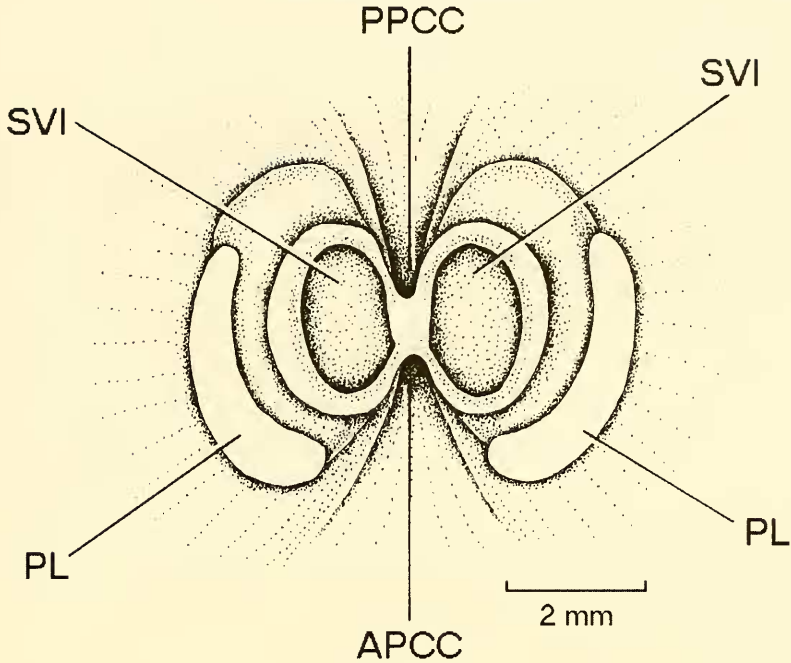


FIG. 5. *Foegia novaezelandiae*. An internal view of the adventitious tube showing the positions of the true shell valves and pallial line lying below the saddle (for abbreviations see pp. 38–39).

the two shell valves and uniting them, is a "saddle" of secondarily secreted shell which has fine concentric growth lines also seen in other clavagelloids (see above). Shell and saddle are sunk into the general fabric of the adventitious tube. A thick, bulbous concretion covers the antero-dorsal region of the right valve, and a second, similarly bulbous concretion is present posteriorly.

Internally, the shell, saddle and adventitious tube of the Dampier specimen (Fig. 5) are united and covered by a smooth calcareous concretion. The positions of the valves appear as depressions surrounded by raised borders of secondarily and internally secreted calcium carbonate. Pockets where anterior and posterior pallial crests are inserted above the valves to create the bulbous secretions covering them are also evident. Two crescentic pallial-line scars encircle the antero-lateral sides of the shell valve impressions. The Pilbarra region of Western Australia is mineral rich and the internal surface of the anterior watering pot was stained brown with iron oxide.

Internal Anatomy

The living animal of *Foegia novaezelandiae* was removed from its tube and is illustrated in Figure 6A–C. The siphons have contracted. The entire body is enclosed in periostracum secreted by the general mantle epithelium. Covering the mantle immediately beneath the true shell and, therefore, approximately encompassing the pericardium, the periostracum is a transparent skin (this is illustrated as a light stippling in Figure 6C). Elsewhere, covering siphons, pedal disc and the general mantle surface, the light brown periostracum is thick and wrinkled. From the dorsal view (Fig. 6A), the pericardium contains a heart, which comprises a central ventricle, penetrated by the rectum, and lateral auricles. Posteriorly, there are paired kidneys, over which the rectum passes. Anteriorly, the visceral mass contains the digestive diverticula and the paired ovaries. From what is the crescentic remnant of a pallial line, pallial retractor muscles pass into the mantle in anterior, ventral and posterior directions to effect

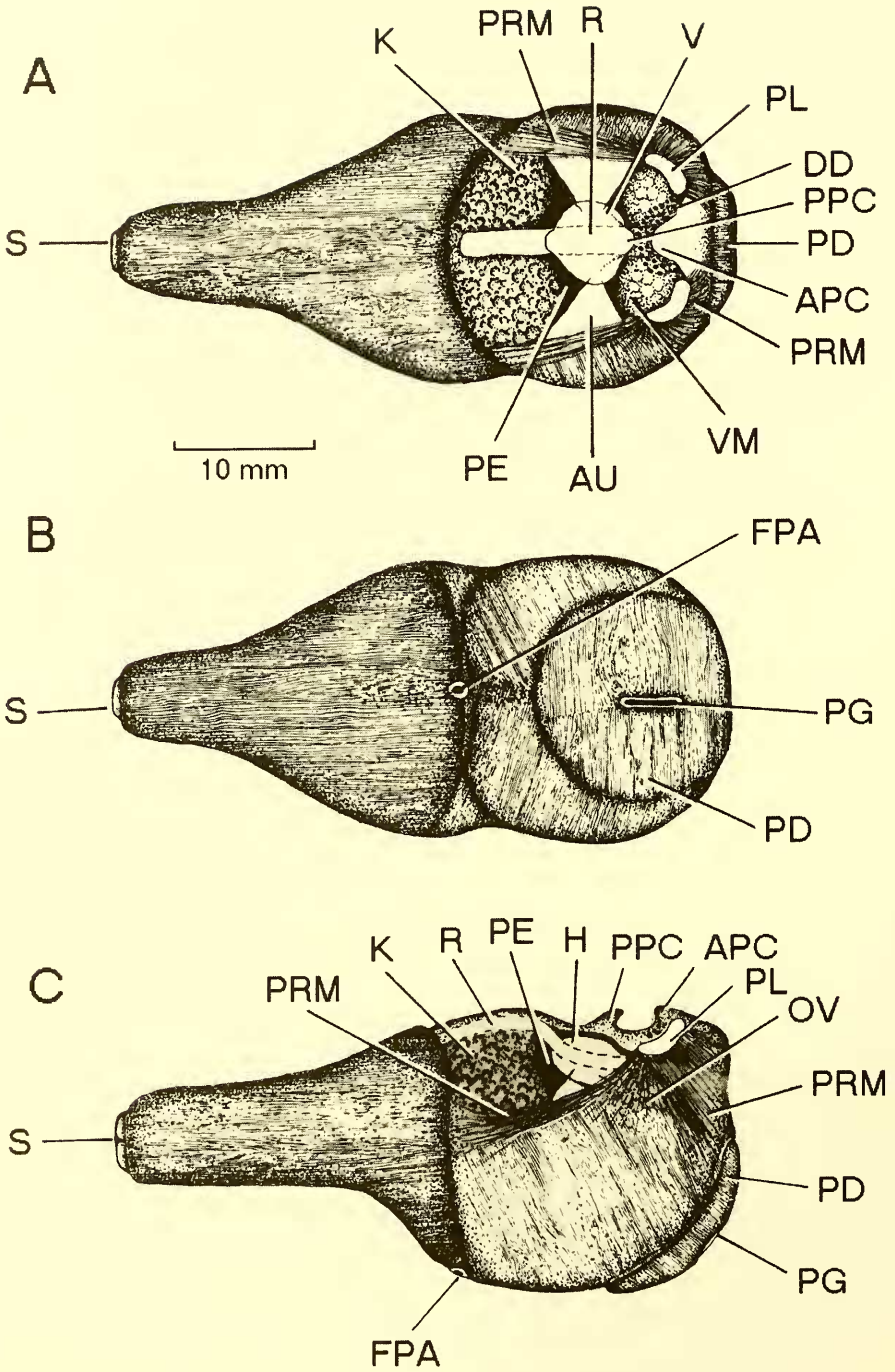


FIG. 6. *Foegia novaezealandiae*. A generalized picture of the anatomy, as seen from A, dorsal; B, ventral and C, right lateral aspects. Note that in C the periostracum surrounding the pericardium is illustrated with a light stippling as in Figure 2C: elsewhere the periostracum is brown, thick and wrinkled (for abbreviations see pp. 38-39).

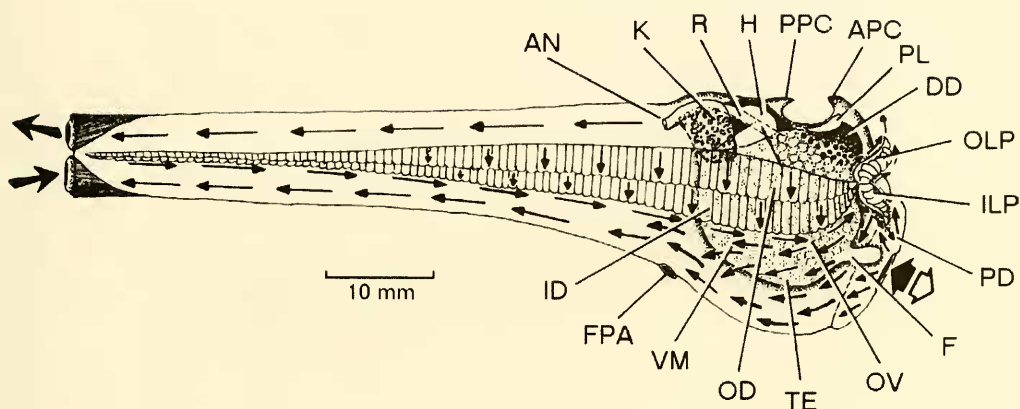


FIG. 7. *Foegia novaezealandiae*. An interval view of the organs and ciliary currents of the mantle cavity as seen from the right side (for abbreviations see pp. 38–39).

contraction of the body within its adventitious tube. There are no other muscles. Also seen dorsally, above the visceral mass, are anterior and posterior pallial crests.

From the ventral view (Fig. 6B), the periostracum-covered pedal disc lies antero-ventrally, and in its centre is a dorso-ventrally aligned pedal gape. Where the siphons meet the remainder of the mantle, there is a mid-ventral fourth pallial aperture. The animal, as seen from the right side (Fig. 6C), shows the heart within the pericardium and the rectum passing over the kidneys, the pallial retractor muscles and the anterior pedal disc and gape. Also seen are the fourth pallial aperture and the anterior and posterior pallial crests.

Organs and Ciliary Currents of the Mantle Cavity

The extended body of *Foegia novaezealandiae* is shown in Figure 7 after being opened on the right side. The most obvious feature is the long paired ctenidia, each of which consists of a complete inner demibranch and the dorsally directed descending lamella only of the outer. The ctenidia extend into the apex of the siphons and thus separate supra- from infra-branchial chambers. The ciliary currents of the ctenidia are of Type E (Atkins, 1937a) and pass collected particles anteriorly towards the mouth in the ctenidial axis and in the ventral marginal food groove of the inner demibranch via small labial palps.

The visceral mass is small with a little foot antero-ventrally. No statocysts have been identified, although they occur in most anomalo-

desmatans (Morton, 1985b), but were similarly not seen in *Dianadema multangularis* (Morton, 2003). Their absence in this specimen may be because only every 10th transverse section was kept but this would mean any missed statocysts would be very small, that is, < 60 μm in length. Within the visceral mass, dorsal ovaries are separate from ventral testes.

The ciliary currents of the visceral mass are directed towards its postero-ventral edge where unwanted particles fall onto the mantle mid-ventrally. As in *Brechites vaginiferus* (Morton, 2002a), the ciliary currents on the internal surface of the pedal disc radiate outwards and downwards from the pedal gape. The ciliary currents on the internal surface of the mantle are downward, complementing those of the visceral mass but, mid-ventrally, strong ciliary currents transfer unwanted material posteriorly, where it is ejected from the inhalant siphon as pseudofaeces. There are also posteriorly directed ciliary currents in the supra-branchial chamber and which presumably help to transfer faeces to the exhalant aperture because the anus is located deep inside the siphons on the posterior surface of the paired kidneys.

Musculature

Foegia novaezealandiae has no adductor and pedal retractor muscles. The pallial line is short, ~ 3 mm, on each side of the body and from it arise pallial retractor muscles that extend anteriorly, ventrally and posteriorly. The attachment of the pallial retractor muscles to the adventitious tube, at the pallial line, is shown in transverse section in Figure 8.

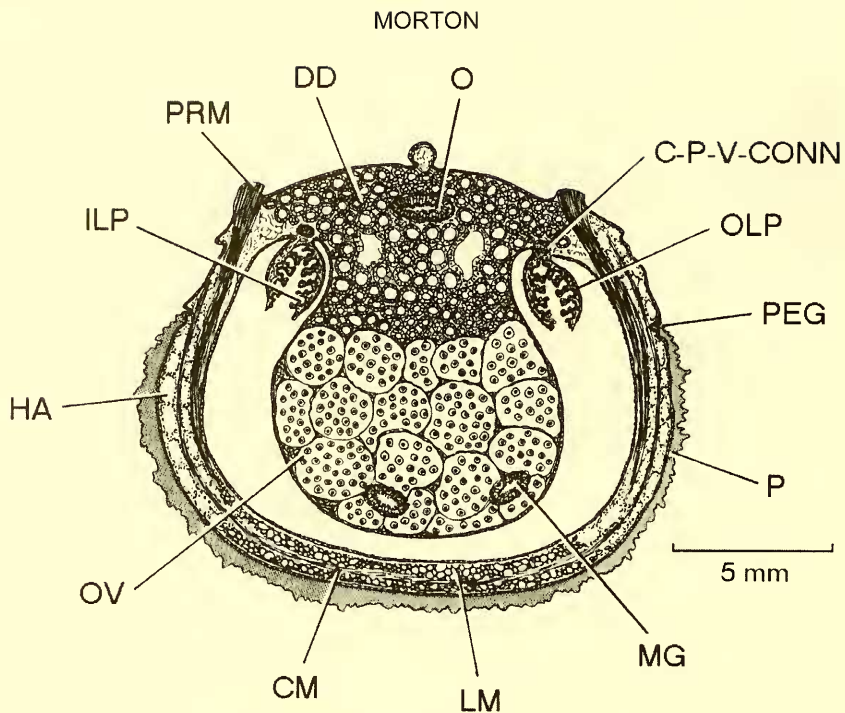


FIG. 8. *Foegia novaezelandiae*. A transverse section through the visceral mass and mantle (for abbreviations see pp. 38-39).

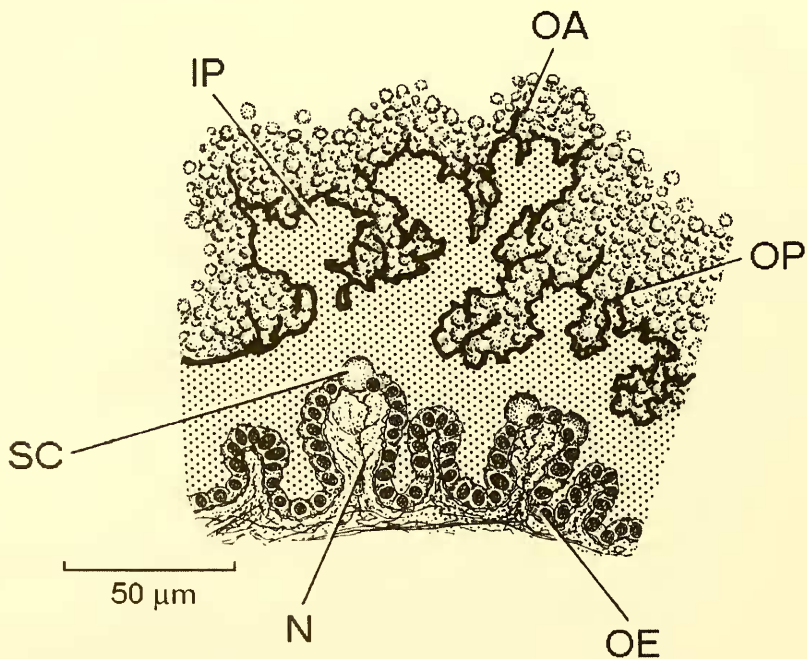


FIG. 9. *Foegia novaezelandiae*. A transverse section through the outer mantle epithelium of the pedal disc showing the periostracum and agglomeration of adhering organic material and bacterial cells (for abbreviations see pp. 38-39).

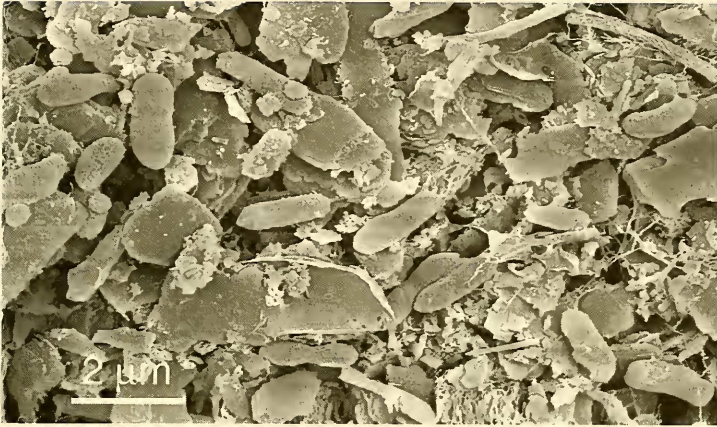


FIG. 10. *Foegia novaezelandiae*. A SEM micrograph of the outer surface of the pedal disc, that is, inside the adventitious tube, showing attached inorganic and organic detritus and rod-shaped bacteria.

Mantle

The mantle margin of *Foegia novaezelandiae* is shown in transverse section in Figure 8. Mantle fusion is of Type C (Yonge, 1982), that is, inner, middle and inner surfaces of the outer mantle folds, so that virtually everywhere the outer surface of the general mantle is enclosed in thick periostracum. The pallial retractor muscles extend into the mantle (Fig. 7) and posteriorly form longitudinal fibres that retract the siphons. Laterally, the mantle has a capacious haemocoel and circular muscles from both the left and right assist in pallial contraction.

The mantle of the pedal disc is shown in transverse section in Figure 9. The outer epithelium is thrown into many folds and at the apex of each pleat there is a swollen cell ~ 8 μm in diameter which is innervated by tiny subepithelial nerves. The epithelium also secretes the periostracum, which comprises two layers. The inner is thick, up to 50 μm and stains blue in Masson's trichrome. It is probably mucoid. The outer layer is thin (2 μm), stains red in Masson's trichrome and is thrown into complex fibrous folds and strands. Around the pedal disc but diminishing towards the siphons, the outer surface of the periostracum is covered in an agglomeration of organic material. Within this are slightly curved, rod-shaped bacteria, ~ 1.5–2 μm in length, and which do not stain in either Masson's trichrome or Ehrlich's haematoxylin, but shine a bright yellow-green. This agglomeration of organic

material and bacteria attached to the pedal disc, being inside the adventitious tube, is in darkness. It is not present in the similarly endobenthic *Brechites vaginiferus* (Morton, 1984a: fig 16a). The agglomeration of inorganic and organic detritus with the bacteria attached to the pedal disc, as seen under the SEM, is illustrated in Figure 10.

Siphons

As is typical of all clavagelloids studied hitherto (Morton, 1984a, b, 2002a, b, 2003), and for other anomalodesmatans (Prezant, 1979b; Morton, 1981b), radial mantle glands at the apices of the siphons of *F. novaezelandiae* produce a secretion which attaches sand grains and other detritus to the thick periostracum of their outer surfaces to camouflage them. The siphons are shown in transverse section in Figure 11A. Internally, there are 16 pallial nerves that, in other clavagelloids, for example, *Brechites vaginiferus* (Morton, 2002a) relate to the number of sensory papillae, which surround the siphonal orifices.

The siphonal wall is illustrated in greater detail in Figure 11B. Externally, are outer and inner layers of the periostracum. Internal to the outer epithelium is a haemocoel and internal to this are successive layers of longitudinal, circular, longitudinal and circular muscles. Criss-crossing the longitudinal muscle blocks are transverse and oblique fibres that must create the tonus which extends and contracts the siphons, in cooperation with the other

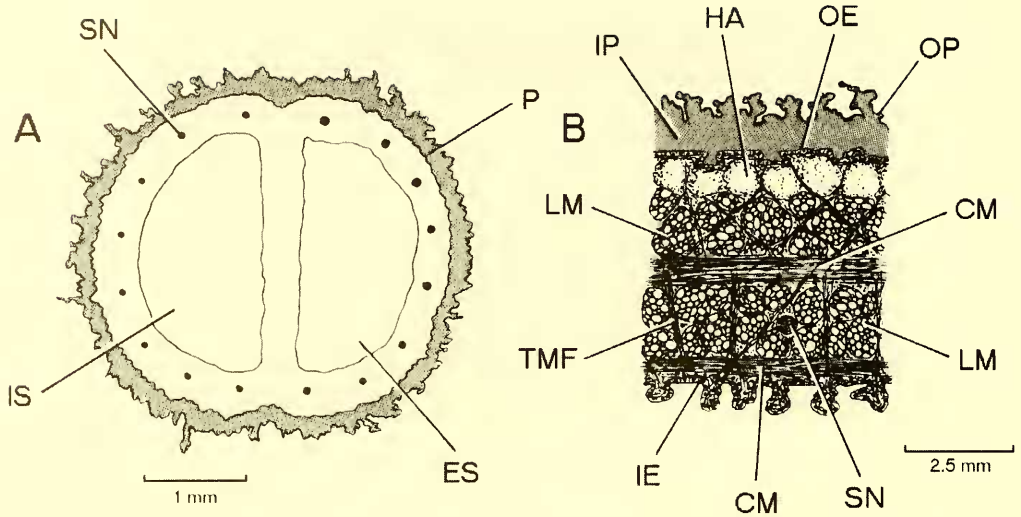


FIG. 11. *Foegia novaezelandiae*. Transverse sections through A, the siphons showing the thick periostracum and pallial nerves and B, the siphonal wall in greater detail (for abbreviations see pp. 38–39).

muscles and blood-filled haemocoels of the mantle. In terms of its muscular complexity, the siphons of *Foegia novaezelandiae* are very similar to those of *Brechites vaginiferus* (Morton, 1984a: fig.14) and *Humphreyia strangei* (Morton, 2002b: fig.12).

Ctenidia

The long, homorhabdic ctenidia (Fig. 7) are also illustrated diagrammatically in transverse section in Figure 12. Approximately five plicae make up the descending lamella of the outer demibranch and about eight both lamellae of the inner. There is a ventral marginal food groove in the latter. Each plica comprises a maximum of 20 filaments anteriorly, but only two as the ctenidia decline in size posteriorly (Fig. 7).

As in other clavagelloids, for example, *Brechites vaginiferus* (Morton, 1984a, 2002a), the epithelium ventral to the kidneys and which forms the dorsal surface of the supra-branchial chamber of the outer demibranch is modified into a hypobranchial gland. The descending lamella of the outer demibranch attaches to the visceral mass by a cuticular junction, as does the ascending lamella of the inner (Atkins, 1937b). This was first described for an anomalodesmatan, that is, *Laternula truncata*, by Morton (1973) and is considered characteristic of all representatives.

Medially, adjacent to the cuticular junction is an osphradium that has not hitherto been described for any anomalodesmatan, although it has been reported in other bivalves, for example, *Corbicula fluminea* (Kraemer, 1981). Left and right osphradia (Fig. 12) extend from the labial palps to the posterior end of the visceral mass. In transverse section (Fig. 13), each osphradium lies between the cuticular junction of the outer demibranch with the visceral mass and the hypobranchial gland. It comprises a central core of cells between which nerve fibres pass towards the periphery. The outer epithelium is thin (4 μm) but periodically along its margin there are swollen sensory cells $\sim 8 \mu\text{m}$ tall and towards which the nerves are oriented.

Pericardium and Kidneys

The pericardium and kidneys are illustrated in Figure 6A and C and in transverse section in Figure 12. The rectum is enclosed by the ventricle of the heart (in turn surrounded by the pericardium) but lies dorsal to the paired kidneys. Each kidney comprises a capacious distal limb and a bag-like proximal limb that opens into the supra-branchial chamber of the inner demibranch at ciliated renal apertures (Fig. 12). There are no pericardial proprioceptors such as occur in *Humphreyia strangei* and *Dianadema multangularis*

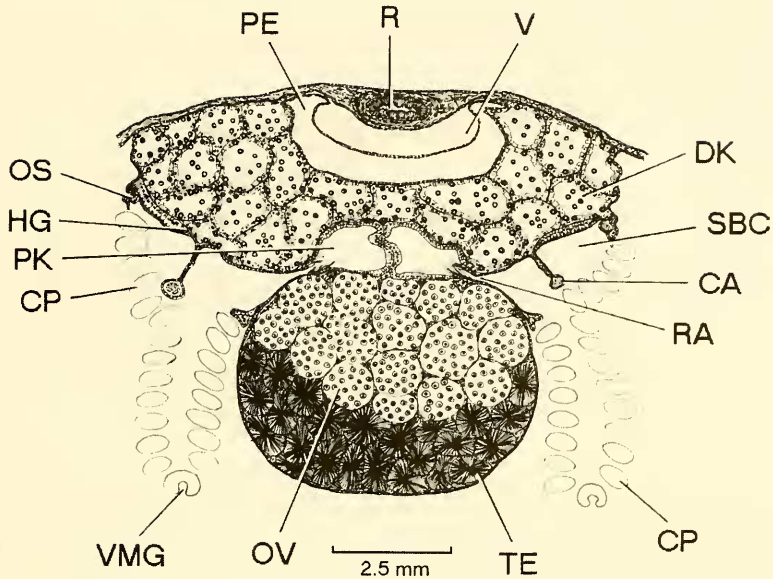


FIG. 12. *Foegia novaezelandiae*. A transverse section through the paired kidneys showing the renal apertures, the ctenidia and the position of the paired hypobranchial glands and osphradia within the supra-branchial chamber of the outer demibranch (for abbreviations see pp. 38-39).

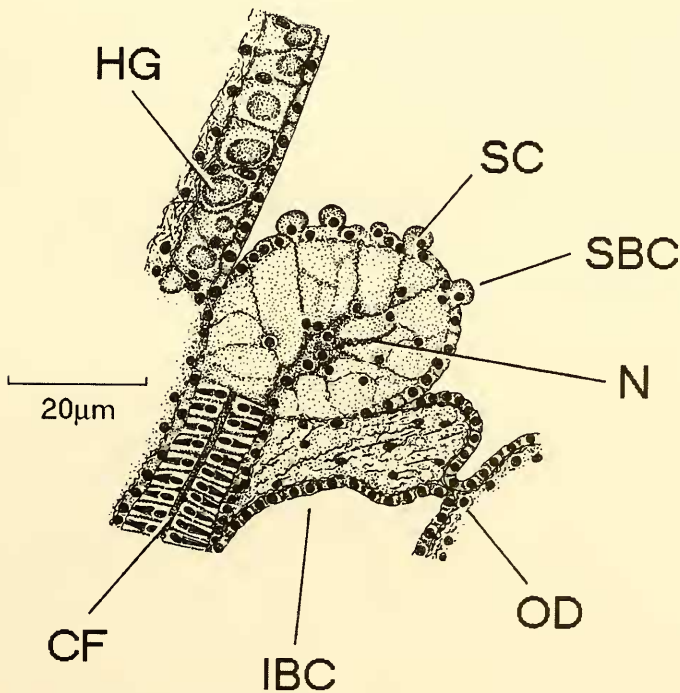


FIG. 13. *Foegia novaezelandiae*. A transverse section through the hypobranchial gland and osphradium in the supra-branchial chamber of the outer demibranch (for abbreviations see pp. 38-39).

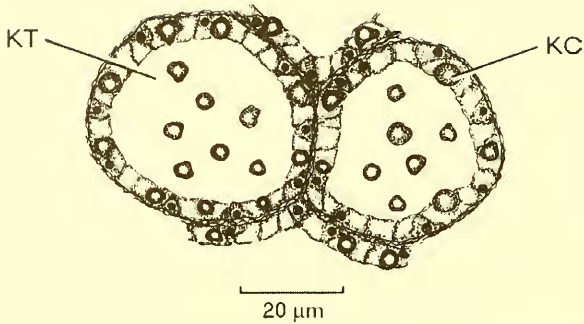


FIG. 14. *Foegia novaezelandiae*. A transverse section through two distal limb tubules of the kidney showing the contained concretions (for abbreviations see pp. 38–39).

(Morton, 2002b, 2003) probably because there are no remnants of the posterior pedal retractor muscles as in *Brechites vaginiferus*, which similarly does not have such sense organs (Morton, 2002a).

Distal kidney tubules are illustrated in transverse section in Figure 14. The cells are some 10 μm tall, largely vacuolated, and contain approximately spherical concretions, between 6–8 μm in diameter and which stain blue in Masson's trichrome but with a lighter staining core. Such concretions also occur in the lumina of the distal limb tubules.

DISCUSSION

The first, detailed description of a tube-dwelling clavagelloid (*Aspergillum dichotomum*) was by Lacaze-Duthiers (1883). Three-quarters of a century later, Purchon (1956, 1960) described *Brechites penis* and, later, Smith (1971, 1976, 1998) produced simple illustrations of Australian species, but not *Foegia novaezelandiae*. Subsequently, Morton (1984a, 2002a, b) described *Brechites vaginiferus* and the cemented *Humphreyia strangei*. Clavagelloids that unite only the left valve into the fabric of a crypt (*Clavagella* and *Bryopa*) have been described by Owen (1835), Soliman (1971) and Morton (1984b). The strange, cemented species, *Dianadema multangularis*, with tubules that form a crown over the dorsal part of the shell and adventitious tube, was described by Morton (2003) and suggested to be similar functionally to the North American, Late Cretaceous *Ascaulocardium armatum* (Pojeta & Sohl, 1987).

Savazzi (1982, 1999) described adaptations of clavagelloids to a tube-dwelling mode of life, and Carter (1978) described how the tubes of gastrochaenids are formed. The gastrochaenids *Cucurbitula* and *Eufistulana* (Morton, 1982, 1983) are convergently very similar to *Dianadema* and *Brechites*, respectively, in forming adventitious tubes. However, the shell valves of gastrochaenids do not unite with the tubes. Also, there is no anterior pedal slit nor are there tubules giving access to interstitial waters. Morton (1984a, 2002a) speculated on the process of tube formation in *Brechites vaginiferus* as, earlier, had Gray (1858b) and Smith (1978). These authors agree that the adventitious tube is secreted but once and that posterior extension is possible either as the animal grows or has to extend itself either to keep pace with an accreting habitat or to effect repair. Because the whole body internal to the tube is covered in thick periostracum, Morton (1984a, 2002a) believed erroneously that the tube of *B. vaginiferus* was created by a secretion produced from glands in the apex of the siphons pouring down the outside of the periostracum-covered adult, between it and the burrow, to form a structure that matched the configuration and surface structure of the burrow wall. Subsequently, Morton (2002b, 2003) showed that the tubes of *Humphreyia strangei* and *Dianadema multangularis* could not be secreted in this way, since both are cemented epibenthically with no burrow template. Formation probably results from the mantle epithelium secreting sequentially either periostracum or adventitious tube, in a manner similar to that described by Savazzi (2000) for the ligament of *Bryopa*.

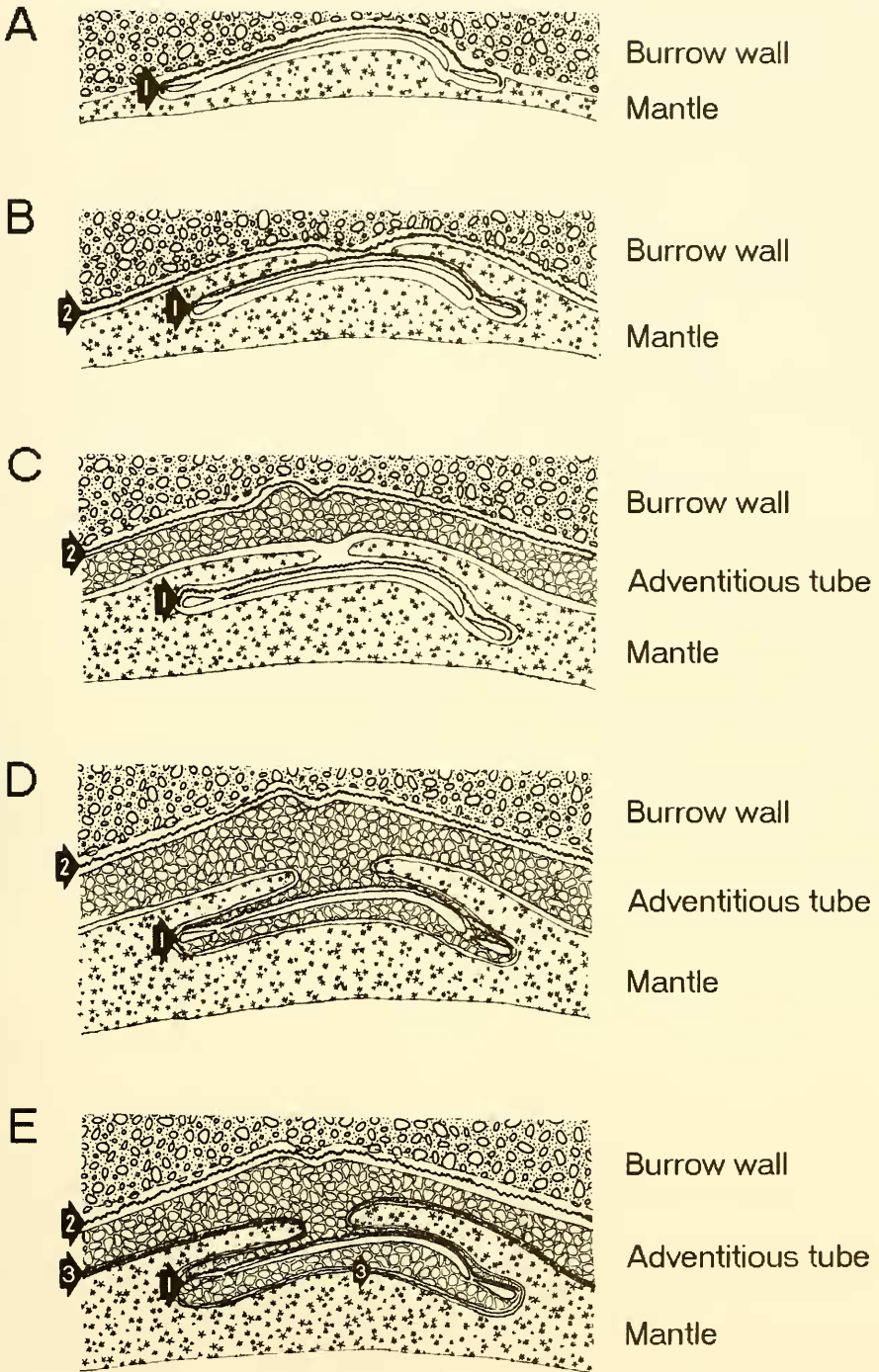


FIG. 15. *Foegia novaezelandiae*. Generalized illustrations of longitudinal sections through the shell, saddle and adventitious tube showing the postulated method of construction (for abbreviations see pp. 38-39).

In *Foegia novaezealandiae* the process of tube formation is more complicated than that of other clavagelloids and is illustrated in Figure 15A–E. Initially, the tube is secreted the same way as in *Brechites vaginiferus* (Morton, 1984a, 2002a), in that the juvenile shell is covered by periostracum: (Fig. 15A, arrow 1). The animal expands hydrodynamically enlarging its burrow to full adult size, and a second layer of periostracum is then secreted by the mantle and covers the whole body. The anterior and posterior pallial crests secrete this too over the tiny shell valves (Fig. 15B, arrow 2). Secretion of periostracum 2 having halted, the adventitious tube is then produced by the mantle (Fig. 15C). Extra secretions of the tube by the pallial crests produce the bulbous protuberances above the true shell valves largely hiding them. Internally too, further secretions by the dorsal mantle unite shell valves, saddle and tube, creating the situation whereby the former are effectively incorporated into the total structure of the adventitious tube (Fig. 15D). Finally (Fig. 15E, arrow 3), a further layer of periostracum is produced by the mantle so that the whole animal, within its tube, is now covered in periostracum which is thin and transparent dorsally (small arrow 3), and thick and wrinkled all over the rest of the mantle (large arrow 3).

The secretion of the adventitious tube of *Foegia novaezealandiae* is thus highly complex involving the mantle in a sequence of secretions of different properties to produce: (i) shell and saddle (covered by periostracum), (ii) a second layer of periostracum, (iii) the main component of the adventitious tube and, finally, (iv) a third layer of periostracum. This results in the peculiar situation wherein the animal is encased within periostracum, within a tube, within periostracum and within a burrow.

The hydrodynamic forces within the mantle and siphons of *Foegia novaezealandiae* which pump the animal up to its full size before production of the adventitious tube and subsequently extend the siphons following contraction, must, as postulated for *Brechites vaginiferus* (Morton, 2002a), in the absence of any adductor muscles, be created by contractions of the pedal disc. In *F. novaezealandiae*, the pedal disc must also create the hydrodynamic forces in the haemocoels of the mantle and siphons, acting agonistically with the circular, longitudinal and transverse muscles within the latter, to effect siphonal extension. The paired supra-bran-

chial osphradia of *F. novaezealandiae* are of interest in this respect. Bivalve osphradia are usually simple structures and generally believed to monitor water flow through the ctenidia (Kraemer, 1981). However, in the case of *F. novaezealandiae*, perhaps they monitor the complex hydrodynamic forces in the mantle cavity and assist in their synchronisation.

Foegia novaezealandiae is also of interest in another respect. The thick anterior covering of periostracum, especially around the pedal disc, is thrown into complex folds not seen in other tube-dwelling clavagelloids, for example, *Brechites vaginiferus* (Morton, 1984a: fig. 12). It also possesses an external covering of an agglomeration of organic material and anucleate "cells". Sand grains and other inorganic detritus covering the siphonal apices exposed to light are not present in the pedal disc agglomeration in the dark. The "cells" are bacteria: might they be sulphide oxidizing? *Foegia novaezealandiae* is unusual in that it occupies hypoxic mud. Is it possible that it has within the base of its tube and into which interstitial water is pumped, a collection of symbiotic bacteria that help to detoxify the sulphide in the incoming water? Might such bacteria also provide it with a supplementary source of nutrition in the form of reduced carbon and amino acids fixed and produced by them, respectively? This may reduce dependence on short-term inputs of organic matter from the tropical, nutrient deficient waters above (Rochford, 1980). This study cannot answer these questions until more intact specimens are available for study.

Reid (1990) surveyed the occurrence of chemoautotrophic sulphide oxidizing bacteria in the Bivalvia and showed that they occur within the ctenidial filaments in specialized bacteriocytes and are characteristic of hydrothermal vent species, for example, *Calyptogena* and *Bathymodiolus*, shallow water representatives of the Lucinoidea (Taylor & Glover, 2000) and Solemyoidea, many of which inhabit sulphur-rich sediments (Dando et al., 1986). *Foegia novaezealandiae* does not have intracellular, ctenidial bacteria, but the record of free-living bacteria with characteristics of sulphide-oxidizing ones on the pedal disc periostracum is of interest and deserves further study.

It is now known that the adventitious tubes of clavagelloids fulfil a number of functions. These are:

- (i) Creating the rigid external skeleton against which the pedal disc can pump interstitial water into and out of the mantle cavity to generate the hydrodynamic pressures necessary in the pallial haemocoels to extend the siphons following retraction.
- (ii) The same pumping action may supply the animal with interstitial bacteria and dissolved organic material and mineral salts, which probably act as sources of nutrients accessory to the material collected by suspension feeding from the tropical, nutrient poor overlying water (Rochford, 1980).
- (iii) Aeration of the interstitial water may be achieved by pumping mantle cavity water obtained from the sea above via the siphons into the burrow heading.
- (iv) Possible detoxification of interstitial water, by burrow aeration.
- (v) Possible detoxification of hydrogen sulphide in the incoming interstitial water by (loosely symbiotic?) chemoautotrophic bacteria and the supply of reduced carbon and amino acids to the host.

Our understanding of the adaptive radiation of the Clavagelloidea increases with each new species studied. It stems from initial, but separate, adaptations in the Cretaceous (Clavagellidae: *Clavagella* and *Dianadema*) and Oligocene (Penicillidae: *Brechites* and *Foegia*) to life within a tube but how such adaptations arose and from what ancestor(s) are unknown (Harper et al., 2000).

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